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TIDAL PERIODICITY IN THE DAILY SETTLEMENT OF INTERTIDAL BARNACLE LARVAE AND AN HYPOTHESIZED MECHANISM FOR THE CROSS-SHELF TRANSPORT OF CYPRIDS

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ABSTRACT

At an intertidal study site in southern California the daily settlement of barnacle cyprids (probably *Chthamalus* spp.) was followed during the summer of 1983. Daily settlement was not significantly cross correlated with wind speed or direction but was significantly cross correlated with the maximum daily tidal range at lags of +1 to +4 days; peak settling occurred several days before the spring tide. This pattern of settlement is nearly identical to that of the megalopa of an intertidal crab, *Pachygrapsus crassipes,* and this suggests that, like these megalopae, cyprids may be transported onshore in slicks over tidally forced internal waves.

INTRODUCTION

Barnacle larvae reside in the plankton for about 3 to 6 weeks (Pyefinch, 1948; Strathmann *et al.,* 1981; Harns, 1984). The terminal larval stage, the cyprid, must migrate* from its location in the pelagic environment back to the shore if it is to continue its development. The quantity of larvae settling at a location can determine the size of the adult population (Connell, 1985; Gaines and Roughgarden, 1985). Thus, the relative success of the cyprids' migration back to the coast may help determine adult abundance.

There seems to be three mechanisms for the cross-shelf movement of cyprids: (1) cyprids swim ashore, (2) chance events deposit cyprids at the shore, and (3) cyprids, by their position in the water column, exploit onshore currents which carry them back to shore.

The swimming speed (several cm/s, Crisp, 1955) and simple sensory system of cyprids would seem to exclude the possibility that they swim ashore. Studies of the daily settlement of cyprids (Bennell, 1981; Kendall *et al.,* 1982; Hawkins and Hartnoll, 1982; Wethey, 1985) suggest that cross-shelf transport is not controlled by chance events. The daily abundance of settlers may be related to the direction of wind driven currents (Bennell, 1981; Hawkins and Hartnoll, 1982) or in contrast, may vary on a lunar cycle (Wethey, 1985). The fact that settlement does not appear to be random with respect to time, but may be related to water movement suggests that cyprids most likely migrate onshore by exploiting onshore currents.

In southern California onshore flow is generated by either the winds or the tides (Winant and Olson, 1976; Winant and Bratkovich, 1981). This is probably true for

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* The definition of migration is that employed by entomologists. "Migration is a persistent, straightened-out movement with some internal inhibition of the responses that will eventually arrest it. It may be effected by the insect's own locomotory exertions or by its active embarkment on some transporting vehicle" (Kennedy, 1961).

most coasts. Evidence that wind generated currents carry cyprids ashore is ambiguous. In one study maximum settling rates occurred during periods of onshore winds (Hawkins and Hartnoll, 1982), but in another it occurred when winds were offshore (Bennell, 1981). None of the studies of daily barnacle settling have attempted to relate the abundance of settlers to tidal phase, although Wethey's (1985) observation of a lunar cycle to settling rate (1985) could alternately have been interpreted as a tidal cycle. The possibility that the tides play a role in the onshore transport of cyprids has not been tested.

In recent papers (Shanks, 1983, 1985a, b; Kingsford and Choat, in press), evidence was presented which suggests that crab megalopae and larvae of other coastal invertebrates and fish are transported from the offshore plankton to the coastline in surface slicks generated over tidally forced internal waves. As the ebbing tide flows across bottom relief such as reefs, banks, and the continental shelf break, lee waves are generated on the thermocline (Rattray *et al.*, 1969; Halpern, 1971; Maxworthy, 1979; Chereskin, 1983). Along the continental shelf the lee wave is formed at the seaward edge of the shelf break (Fu and Holt, 1982). When the ebbing current goes slack, the lee wave is released and progresses shoreward as a series of large amplitude internal waves (Chereskin, 1983). The slicks are surface manifestations of currents generated over the tops of these internal waves (Ewing, 1950) and they delineate a zone of converging and downwelling currents situated over the trough of the waves (Fig. 7 in Zeldis and Jillett, 1982). As the internal waves travel shoreward the wave-generated currents sweep oil and flotsam into the convergence forming a slick (Ewing, 1950). Buoyant flotsam will remain at the surface trapped in the convergence and be carried along with the waves (Arthur, 1954; Shanks, 1983). The proposed mechanism of larval transport suggests that any organism which can maintain itself at the surface in the face of downwelling currents at the convergence will, like the flotsam, remain in the slick and be transported ashore (Shanks, 1983).

The purpose of this research was to investigate the mechanism of onshore transport of barnacle larvae. Onshore transport was not directly investigated, but was inferred from correlations of daily settlement of cyprids in the intertidal zone with physical factors in the environment which cause onshore flow:winds and tides. For daily settlement to be related to onshore transport cyprids must settle immediately upon reaching the shore and there must be an offshore reservoir of larvae which can be periodically swept onshore. Gaines *et al.* (1985) found that the abundance of planktonic *Balanus glandula* cyprids in the waters above an intertidal zone decreased dramatically with proximity to the shore while the abundance of similarly sized copepods did not decrease shoreward. They interpret this decrease in planktonic cyprids as due to their settling out upon contacting the bottom as they were swept through the intertidal. The planktonic stage in the life cycle of barnacles has received little attention and there are few published descriptions of their offshore distribution. Crisp and Southward (1958) and Kendell *et al.* (1985) both found an abundance of cyprids out to about 10 km off the coast of England and I have made similar observations in the Southern California and South Atlantic Bights (pers. obs.). These studies suggest that there is an offshore reservoir of cyprids and that cyprids settle soon after reaching the shore. Hence, the assumption that the pattern of daily settlement of cyprids is related to the forces carrying the cyprids onshore seems reasonable.

MATERIALS AND METHODS

Barnacle settlement was studied in the intertidal zone 1.5 km north of the Scripps Institution of Oceanography pier (35°5′N, 177°5′W). Winter and spring storms remove sand from this stretch of beach leaving a boulder/cobble field resting on a smooth shelf of sandstone. Sand accumulates during the late spring and summer until just the larger boulders protrude above the surface of the beach. From about 0 to 1.6 m above mean lower low water (MLLW) the dominant fauna on the boulders is the barnacle *Chthamalus* spp., which carpets many boulders almost completely. The tides are semidiurnal with a maximum range of nearly 3 m. The shore is protected from ocean swells by refraction of waves away from the study site due to a submarine canyon located immediately offshore (the Scripps Canyon). Maximum significant wave height (*i.e.*, average of larger one-third of the waves) measured at the Scripps pier was 1 m or less during the study.

Barnacle settling plates initially consisted of pancakes of Splash Zone® epoxy glued to the seaward face of large boulders located at +1.5, +1.0, and +0.3 m MLLW (Rocks 1, 2, and 3 respectively). Into each pancake three circular grooves (4 cm dia × 0.5 cm wide, surface area per groove 3 cm^2) were pressed. During a second period of observations a piece of plain ceramic floor tile was glued with the grooved bottom side up (3 grooves, 5 cm long × 0.5 cm wide, surface area per groove 2.5 cm^2) on the seaward side of Rock 2 (+1.0 m MLLW).

Counts were made daily between 9 April and 30 June, 1983, and 17 August and 1 November, 1983, during daytime low tides. Observations of settlement on Rock 3 stopped on 18 May (after 41 days) because the rock was buried by sand. During the second observation period settling was only followed at Rock 2. With the aid of 10× hand lens counts were made of the cyprids and newly metamorphosed barnacles present in the grooves on the settling plates. Barnacles were not identified to species, but given the extreme dominance of the boulders by *Chthamalus* spp. most of the settlers were probably *Chthamalus.* Following each daily count the grooves were vigorously brushed with a coarse brush which removed all visible (as viewed with a 10× hand lens) remains of cyprids and barnacles.

Cross correlations using the methods of Blackman and Tukey (1959) were calculated between the daily barnacle settlement and both wind direction and maximum daily tidal range. Wind direction data were taken from the records of the National Weather Service station at Lindberg Field, San Diego, California. Wind direction measured at this location is usually not different from that observed at Scripps pier (C. Winant, pers. comm.). Tidal range was taken as the maximum daily difference between a high tide and the next low tide during a 24 h period beginning at 18:00 h. Calculations of cross correlations were limited to lags of ±10% of the record length (Otnes and Enochson, 1978).

Before calculating the cross correlations, daily barnacle settlement was scaled to the hours of submersion at each tidal height. The purpose of these calculations was to control for variation in the duration of submersion over the semilunar tidal cycle that may have effected settlement in addition to semilunar tidally driven currents. The rate of barnacle settling steadily decreased during each observation period. Therefore the data were also detrended prior to the calculation of the cross correlations. Detrending (Otnes and Enochson, 1978) was accomplished as follows: a linear regression was calculated between the log of the barnacle settlement/h submersion/day and sampling sequence (*e.g.*, time); then the residuals from each day's datum were subtracted from the overall average daily settling rate (log of barnacle settlement/h of submersion/day) during the period of observation to give the detrended values.

RESULTS

During both sampling periods and at all tidal heights there was a clear rhythm to the daily abundance of settlers and this rhythm appeared to be related to the maximum daily tidal range (Figs. 1, 2). The period separating maximum barnacle settlement (starred data points in Figs. 1, 2) was not different from the period separating the maximum spring tide (Table I). Moreover, during the first sampling period the time separating maximum spring tides alternated between about 12 and 17 days as did the time between maximum barnacle settlement.

Inspection of Figures 1 and 2 suggests that peak settlement usually occurred one to several days before the spring tide. The results of the cross correlation calculations support this impression (Figs. 3, 4). Significant ($P < 0.01$) cross correlations occurred around +1 and +4 days lag. That is, maximum barnacle settlement occurred 1 to 4

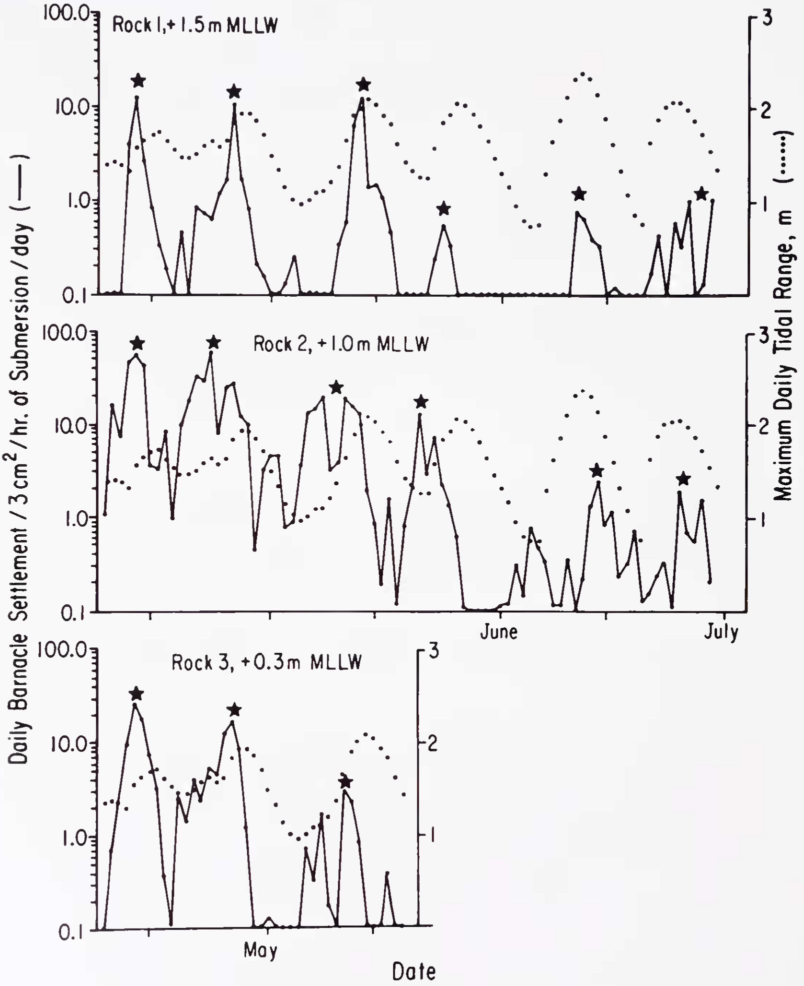

FIGURE 1. Daily barnacle settling rate (number/3 cm^2/h of submersion/day, solid line) at three tidal heights (+1.5, +1.0, and +0.3 m MLLW) plotted with the maximum daily tidal range in meters (dotted line). Data were collected from 9 April to 30 June, 1983, at Dike Rock, California. Stars over the plot of daily barnacle settling rate indicate dates of peak settlement. The small increase in settling rate which occurred around 5 June was not considered to be a peak in settlement because it was a tenth the size of the preceding peaks and only a third the size of the following two peaks.

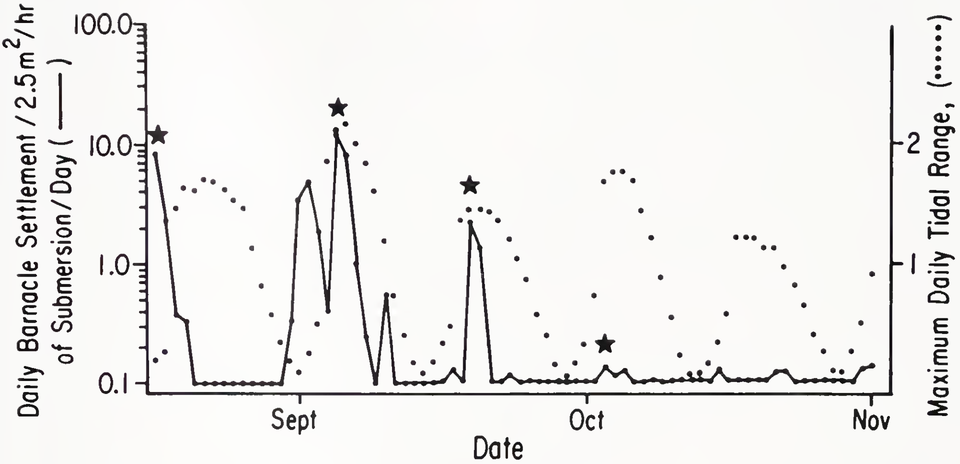

FIGURE 2. Daily barnacle settling rate (number/2.5 cm^2/h of submersion/day, solid line) at +1.0 m MLLW plotted with the maximum daily tidal range in meters (dotted line). Data were collected from 17 August to 1 November, 1983, at Dike Rock, California. Stars over the plot of daily barnacle settling rate indicate dates of peak settlement.

days before the maximum spring tide. From about 12% (Fig. 3, Rock 2) to 40% (Fig. 3, Rock 3) of the variation in barnacle settlement might be attributable to effects of the semilunar tidal cycle. Scaling the daily barnacle settlement by hours of submersion may have injected a tidal periodicity into the data. However, the detrended, but not scaled data (*i.e.*, number/day) also displayed similar significant cross correlations between settlement rate and the daily tidal range.

Through May in the first set of observations, maximum settlement at Rocks 1 and 2 occurred between the neap and spring tides. Around the end of May the timing of the peak settlement appears to shift such that it occurred at or just after the spring

TABLE I

Comparison of the period in days separating maximum spring tide and peaks in daily barnacle settling rate

	Period (days) between maximum spring tide and maximum barnacle settlement[1]					
	First sampling period (9 April–30 June, 1983)				Second sampling period (17 Aug.–1 Nov., 1983)	
Period	Tide	Rock 1	Rock 2	Rock 3	Tide	Rock 2
1	11	13	10	13	15	17
2	17	17	16.5	15	14	14
3	12	11	12.5	—	14	14
4	17	18	24	—		
5	12	16.5	11	—		
Mean	13.8	15.1	14.8	14.0	14.3	15.0
SE	1.3	1.3	2.6	1.0	0.3	1.0

[1] Days of peak barnacle settlement are labeled with stars in Figures 1 and 2.

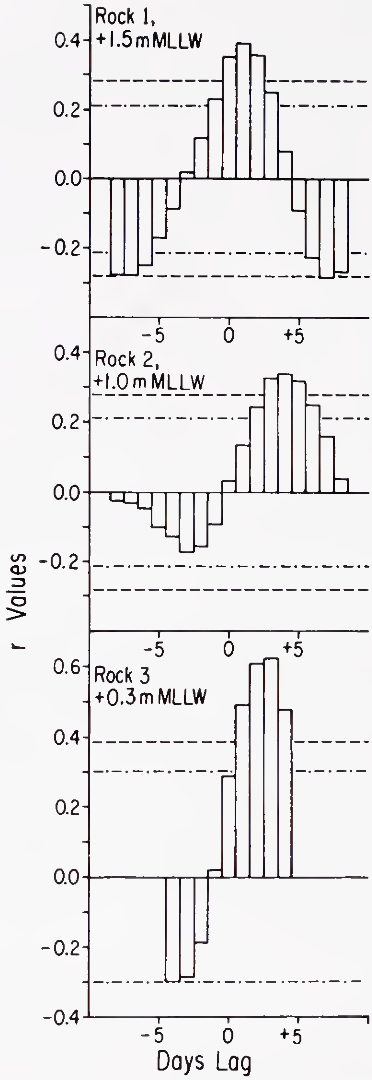

FIGURE 3. Cross correlations at three tidal heights (+1.5, +1.0, and +0.3 m MLLW) of the detrended daily barnacle settlement (Log (X + 1)/3 cm^2/h of submersion/day) *versus* the maximum daily tidal range. Data were collected over the period 9 April to 30 June, 1983. Cross correlation was limited to ±10% of the length of the time series (Otnes and Enochson, 1978). Critical $r_{0.05}$ (–•–) and $r_{0.01}$ (– – –) are also plotted.

tides (Fig. 1). There was also a sharp decrease in the rate of settlement which occurred at this time. This apparent shift was associated with a sharp drop in the sea surface temperature from about 18.5°C to about 14.5°C (Fig. 5).

There was no obvious correlation between wind direction and the daily rate of barnacle settlement (for example, Fig. 6). There were no significant cross correlations between the rate of barnacle settlement and either the resultant wind direction for an entire day (*i.e.,* the vector sum of wind speeds and directions measured every 3 h divided by the number of observation) or the wind direction during high tides. Set-

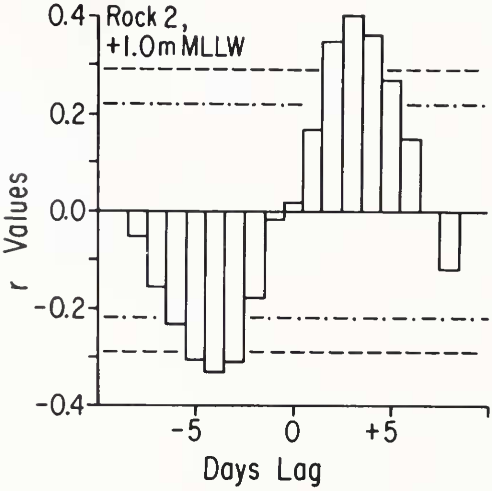

FIGURE 4. Cross correlation at +1.0 m MLLW of the detrended daily barnacle settlement (Log (X + 1)/2.5 cm^2/h of submersion/day) vs the maximum daily tidal range. Data were collected over the period 17 August to 1 November, 1983. Cross correlation was limited to ±10% of the record length (Otnes and Enochson, 1978). Critical $r_{0.05}$ (– • –) and $r_{0.01}$ (– – –) are also plotted.

tlement was not significantly different (*t*-test, $P > .10$) on days with onshore winds (winds from about 204 to 280°) than days with longshore winds. Resultant winds blowing offshore (winds from around 90°) did not occur during either observation period nor were there strong near shore winds.

DISCUSSION

At all three tidal heights and during both observation periods the daily settlement of barnacles was significantly cross correlated with the maximum daily tidal range. Maximum settling tended to occur one to four days before the spring tide. This relationship between daily settling rate and the semilunar tidal cycle is almost identical to that observed for settling of *Pachygrapsus crassipes* megalopae (Shanks, 1983, 1985b). Peak catches of these megalopae also tended to occur four days before the spring tide. The megalopae of *P. crassipes* are a larval form which is transported onshore in slicks over tidally forced internal waves (Shanks, 1983, 1985a). The similarity between the fortnightly cycle of barnacle settling and that of the *P. crassipes* megalopae suggests that the barnacle cyprids settling in the Dike Rock intertidal may also be carried ashore by internal waves.

On the southern California continental shelf the internal waves have a fortnightly cycle related to tidal range (Cairns, 1967, 1968). The largest waves, generated during spring tides, break and progress across the shelf as internal bores, producing near-bottom onshore flow and surface offshore flow (Winant and Olson, 1976; Winant and Bratkovish, 1981). The internal bores also produce turbulence which disrupt and weaken the thermocline on which subsequent internal waves propagate (Cairns, 1968). During tides with smaller range, trains of internal waves of lesser magnitude are formed which propagate across the shelf into shallow water (Cairns, 1968; Winant, 1974). If cyprids were using broken internal waves as a means of shoreward transport, one would expect maximum settlement around the spring tide when internal bores are present. But peak settlement consistently occurred several days before spring tide. This

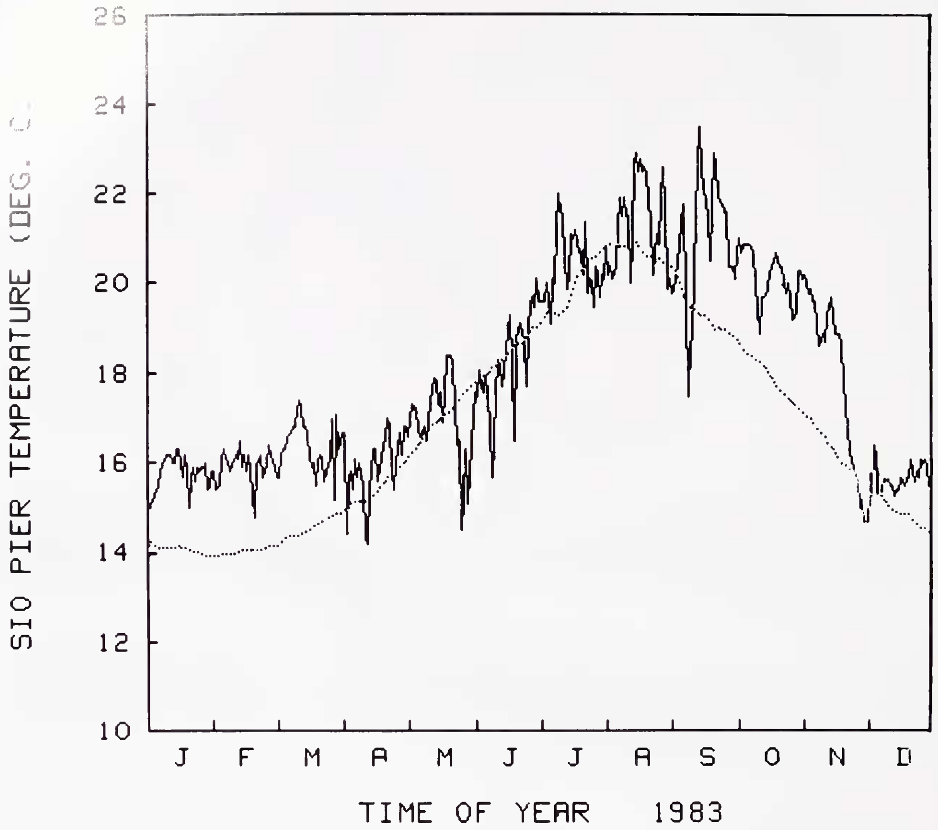

FIGURE 5. The daily sea surface temperature for 1983 (solid line) measured 1.5 km from the Dike Rock study area at the Scripps Institution of Oceanography pier. The dotted line is the 62 year mean sea surface temperature.

suggests that these cyprids may be transported onshore by the unbroken internal waves. High settlement of cyprids and megalopae did not occur during the periods between the spring and neap tides, periods when smaller internal waves ought to have been formed. The data presented in Shanks (1983) indicate that only some sets of internal waves cause onshore transport. Perhaps those internal waves produced during the periods between the spring and neap tides, due to the weakened thermocline, do not cause onshore transport.

A variety of physical factors effect the formation of these tidally generated internal waves (*e.g.*, tidal range, type of bottom topography, and water column density structure). The waters offshore of Dike Rock are characterized by mesotides (tidal range 2–4 m, Davies, 1964), a submarine canyon, narrow shelf (<3 km), and seasonally shallow thermocline (Cairns and Nelson, 1970). While onshore transport of larvae by internal waves occurs on other coasts (*e.g.*, New Zealand, Kingsford and Choat, in press; the South Atlantic Bight, pers. obs.) the pattern of daily settlement need not be similar to that observed at Dike Rock. This is because the physical environment in which the waves are formed will vary from site to site. My preliminary observations in the South Atlantic Bight, an area of microtides (tidal range < 2 m), suggest that

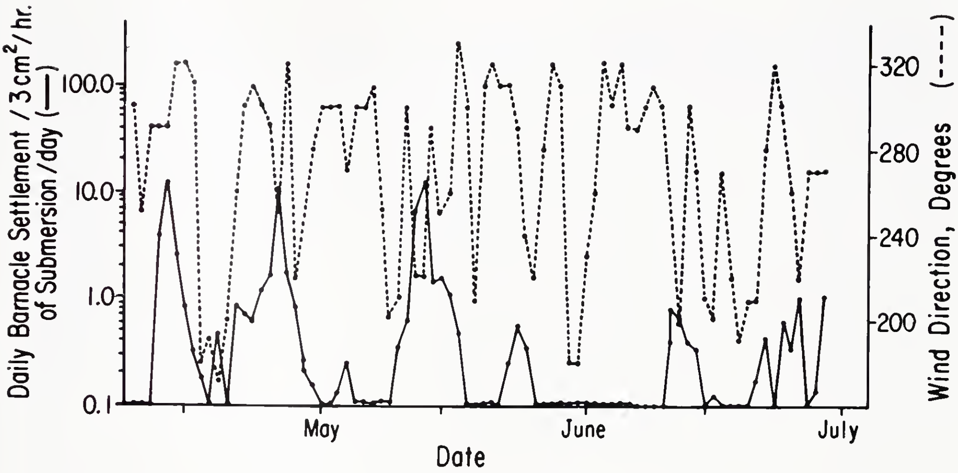

FIGURE 6. Daily barnacle settling rate (number/3 cm^2/h of submersion/day, solid line) at +1.5 m MLLW plotted with the daily resultant wind direction (dashed line). Wind direction is the direction from which the wind is blowing. Onshore winds come from around 270°. Settlement data were collected from 9 April to 30 June, 1983, at Dike Rock, California.

onshore-transporting internal waves are only formed around the spring tide and I would predict that settlement of organisms transported by these waves would be highest during these periods.

For an organism to utilize slicks over internal waves as a mechanism of onshore transport, it is necessary for it to remain at or near the surface. The megalopae of *P. crassipes* display a set of behaviors—positive phototaxis, negative geotaxis, high baro- and photokinesis, high swimming speed (9 cm/s), and high thigmokinesis (Shanks, 1985a)—which aid them in locating and remaining at the ocean's surface. The behaviors associated with the planktonic existence of cyprids have not been well studied but the behaviors which have been observed—positive phototaxis (Knight-Jones, 1953; Crisp, 1955; Crisp and Ritz, 1973), fairly high swimming speeds (4 to 5 cm/s, Crisp, 1955), and high barokinesis (Knight-Jones and Morgan, 1966)—are all behaviors which may, as they do for *P. crassipes* megalopae, aid cyprids in locating and remaining in the surface waters where transport by slicks can occur. In addition, the cyprids of some species are hydrophobic and may remain at the ocean's surface by sticking to the surface film (Knight-Jones, 1953; Crisp, 1955; Connell, 1956). However, actual contact of an organism with the ocean's surface is not necessary for internal-wave mediated transport to occur. The only available data on the vertical distribution of cyprids in the water column are those of De Wolf (1973) and Grosberg (1982). De Wolf (1973) found little vertical stratification of cyprids in a tidally well mixed estuary while Grosberg (1982), who collected samples in a small, poorly mixed harbor, found that cyprids of *Balanus glandula* were concentrated at the water surface (<0.5 m depth) while the cyprids of *B. crenatus* lived somewhat deeper (>2 m depth). I know of no published data on the vertical distribution of cyprids in offshore waters.

The observed correlation of settling rate with the tides might be due to the timing of adult spawning coupled with the rate of larval development. If, as has been observed in some crab populations (Christy, 1982), adult barnacles spawn on a fortnightly tidally timed cycle and the subsequent larval development is around two weeks, or some multiple thereof, then a similar cycle of larval settling in the intertidal might be observed. Even if adult *Chthamalus* spp. do spawn on a rigid fortnightly schedule (there is no evidence for or against this) larval development time is probably so variable as to mask the effect of adult spawning sychrony by the time the larvae are ready to settle. Development time has not been measured in *Chthamalus* spp., but it has for *Balanus glandula,* a species which occupies the same habitat and range as *Chthamalus* spp. (Morris *et al.,* 1980). Strathmann *et al.* (1981) found development times from release to cyprid ranging from 10 days at 17°C to 22 days at 9.5°C while cyprids could delay metamorphosis for from 19 to 35 days at temperatures of 17 and 9.5°C, respectively. During the first series of observations the temperature at the Scripps Institution of Oceanography pier varied from 18.5 to 14°C and during the second set from 22.5 to 18.5°C (Fig. 5). Despite these temperature variations, the period separating peaks in larval settlement was not significantly different from the period separating spring tides (Table I). Thus, it would seem that the duration of larval development is too variable to support the hypothesis that the observed discrete fornightly settlement cycle simply reflects the cycle of adult spawning.

Although the possibility that the daily rate of settling of barnacles is related to the semilunar tidal cycle has not previously been reported there are some data in the literature which support this observation. Wethey (1985) followed daily settlement of *Semibalanus balanoides* during two different settling seasons on the coast of Massachusetts. He found no relationship between daily settlement and wind direction, but he did note an apparent lunar periodicity to settling which might, in fact, be related to the semilunar tidal cycle. Peak settlement tended to occur several days before and after spring tides. Both Wethey (1985) and Kendall *et al.* (1982) followed daily settlement at intertidal stations along the Yorkshire coast, U.K. In Wethey's observations at three sites (Staithes, Robin Hood's Bay, and Filey) there is no obvious tidal periodicity to settlement, but in Kendall *et al.* (1982) daily settlement at Robin Hood's Bay (Fig. 2, Kendall *et al.,* 1982) does appear to vary on a tidal cycle: peak settling rates occurred between the neap and spring tides as was observed in this study. These studies suggest that in other areas daily barnacle settlement may be related to the semilunar tidal cycle.

Two studies, both from the Irish Sea, present data which suggest that daily settling rate was related to wind direction. In Hawkins and Hartnoll (1982) peak settling in 1979 occurred during onshore winds, while Bennell (1981), during the same 1979 season, suggests that peak settling rate occurred during offshore winds. There was no apparent tidal periodicity to the settling rate in either study. If cyprids of intertidal barnacles are carried onshore by tidally driven internal waves then perhaps the extreme tidal mixing which occurs over much of the Irish Sea (an area of macrotides, >4 m) and the complex distribution of marine fronts at either end of the sea (Simpson and Hunter, 1974; Simpson and Pingree, 1978) prevent the propagation of internal waves through the Irish Sea. In the absence of internal waves, the effects of wind direction on settling rate may then become apparent.

Additional data that bear on the mechanism of onshore transport are hard to come by. Attempts to correlate previous records of daily barnacle settling (Bennell, 1981; Hawkins and Hartnoll, 1982; Kendell *et al.,* 1982; Wethey, 1985) with either wind direction or tidal range are hampered by the shortness of the time series. These studies followed the settling of *Semibalanus balanoides,* a species with a brief springtime settling season. The longest record (Hawkins and Hartnoll, 1982) is only 60 days and the average published record is only 30 days. Correlations between such short time series and wind direction are probably acceptable. Wind events are usually only several days in duration (for example see Fig. 6), and, there might be 10 or more wind events during a month-long time series against which settling rate can be compared. For correlation against the semi-lunar tidal cycle the records are usually too short. If peak settling rates occur between the neap and spring tides, as was observed in this study, then the average time series will only contain two such periods. In this situation, cycles of tidal range and settling rate must be closely related (see for example Rock 3 this study where the time series is only 42 days) if significant correlations are to be found. If a species with a longer settling season had been studied perhaps a tidal periodicity to settling rate would be a more common observation.

The data presented in this paper suggest an hypothesis to explain the onshore migration of cyprids; they are transported onshore in slicks over tidally forced internal waves. From this hypothesis several predictions can be made and used to test the hypothesis. If cyprids, or any other larvae, are transported onshore in internal-wave slicks, then they must inhabit the surface waters. Further, if the hypothesis is correct, then in the waters over those internal waves which are causing onshore transport of surface drifters (Shanks, 1983), cyprids should be most abundant in the internal-wave slicks. Finally, if internal waves are 'catching' cyprids and carrying them shoreward, then there should be significantly fewer cyprids at the surface immediately behind a set of internal waves than immediately in front of the set.

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LITERATURE CITED

ARTHUR, R. S. 1954. Oscillations in the sea temperature at Scripps and Oceanside piers. *Deep Sea Res.* **2:** 129–143.

BENNELL, S. J. 1981. Some observations on the littoral barnacle populations of north Wales. *Mar. Environ. Res.* **5:** 227–240.

BLACKMAN, R. B., AND J. W. TUKEY. 1959. *The Measurement of Power Spectra.* Dover, NY. 190 pp.

CAIRNS, J. L. 1967. Asymmetry of internal tidal waves in shallow coastal waters. *J. Geophys. Res.* **72:** 3563–3565.

CAIRNS, J. L. 1968. Thermocline strength fluctuations in coastal waters. *J. Geophys. Res.* **73:** 2591–2595.

CAIRNS, J. L., AND K. W. NELSON. 1970. A description of the seasonal thermocline cycle in shallow coastal water. *J. Geophys. Res.* **75:** 1127–1131.

CHERESKIN, T. K. 1983. Generation of internal waves in Massachusetts Bay. *J. Geophys. Res.* **88:** 2649–2661.

CHRISTY, J. H. 1982. Adaptive significance of semilunar cycles of larval release in fiddler crabs (genus *Uca*): test of an hypothesis. *Biol. Bull.* **163:** 251–263.

CONNELL, J. H. 1956. A study of some factors which determine the density and survival of natural populations of the intertidal barnacle, *Balanus balanoides* (L.). Ph.D. thesis, Univ. of Glasgow, Scotland, 135 pp.

CONNELL, J. H. 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *J. Exp. Mar. Biol. Ecol.* **93:** 11–46.

CRISP, D. J. 1955. The behaviour of barnacle cyprids in relation to water movement over a surface. *J. Exp. Biol.* **32:** 569–590.

CRISP, D. J., AND A. J. SOUTHWARD. 1958. The distribution of intertidal organisms along the coasts of the English Channel. *J. Mar. Biol. Assoc. U.K.* **37:** 157–208.

CRISP, D. J., AND D. A. RITZ. 1973. Responses of cirripede larvae to light. I. Experiments with white light. *Mar. Biol.* **23:** 327–335.

DAVIES, J. L. 1964. A morphogenic approach to world shorelines. *Zeit. Fur Geomorphol.* **8:** 127–142.

De Wolf, P. 1973. Ecological observations on the mechanisms of dispersal of barnacle larvae during planktonic life and settling. *Neth. J. Sea Res.* **6**: 1–129.

Ewing, G. 1950. Slicks, surface films and internal waves. *J. Mar. Res.* **9**: 161–187.

Fu, L.-L., and B. Holt. 1982. Seasat views oceans and sea ice with synthetic-aperture radar. *Jet Propulsion Lab. Publ.* 81–120, Pasadena, Calif.

Gaines, S., and J. Roughgarden. 1985. Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proc. Natl. Acad. Sci. USA* **82**: 3707–3711.

Gaines, S., S. Brown, and J. Roughgarden. 1985. Spatial variation in larval concentration as a cause of spatial variation in settlement for the barnacle *Balanus glandula*. *Oecologia* **67**: 267–272.

Grosberg, R. K. 1982. Intertidal zonation of barnacles: the influence of plankton zonation of larvae on vertical distribution of adults. *Ecology* **63**: 894–899.

Halpern, D. 1976. Observations on short-period internal waves in Massachusetts Bay. *J. Mar. Res.* **37**: 116–132.

Harns, J. 1984. Influence of water temperature on larval development of *Elminius modestus* and *Semibalanus balanoides* (Crustacea, Cirripedia). *Helgol. Meeresunters.* **38**: 123–134.

Hawkins, S. J., and R. G. Hartnoll. 1982. Settlement patterns of *Semibalanus balanoides* (L.) in the Isle of Man (1977–1981). *J. Exp. Mar. Biol. Ecol.* **62**: 271–283.

Kendall, M. A., R. S. Bowman, P. Williamson, and J. R. Lewis. 1982. Settlement patterns, density and stability in the barnacle *Balanus balanoides*. *Neth. J. Sea Res.* **16**: 119–126.

Kendall, M. A., R. S. Bowman, P. Williamson, and J. R. Lewis. 1985. Annual variations in the recruitment of *Semibalanus balanoides* on the north Yorkshire coast 1969–1981. *J. Mar. Biol. Assoc. U.K.* **65**: 1009–1030.

Kennedy, J. S. 1961. A turning point in the study of insect migration. *Nature* **189**: 785–791.

Kingsford, M. J., and J. H. Choat. In press. The influence of surface slicks on the distribution and onshore movement of small fish. *Mar. Biol.*

Knight-Jones, E. W. 1953. Laboratory experiments on gregariousness during setting in *Balanus balanoides* and other barnacles. *J. Exp. Biol.* **30**: 584–588.

Knight-Jones, E. W., and E. Morgan. 1966. Responses of marine animals to changes in hydrostatic pressure. *Ann. Rev. Oceanogr. Mar. Biol.* **4**: 267–299.

Maxworthy, T. 1979. A note on the internal solitary waves produced by tidal flow over a three-dimensional ridge. *J. Geophys. Res.* **84**: 338–345.

Morris, R. H., D. P. Abbott, and E. C. Haderlie. 1980. *Intertidal Invertebrates of California*. Stanford University Press, Stanford, CA. 690 pp.

Otnes, R. F., and L. Enochson. 1978. *Applied Time Series Analysis. Vol. 1. Basic Techniques*. Wiley & Sons, NY. 449 pp.

Pyefinch, K. A. 1948. Notes on the biology of Cirripedes. *J. Mar. Biol. Assoc. U.K.* **27**: 464–503.

Rattray, M. Jr., J. G. Dworski, and P. E. Kovala. 1969. Generation of long internal waves at the continental slope. *Deep Sea Res.* **16**: 179–195.

Shanks, A. L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. *Mar. Ecol. Prog. Ser.* **13**: 311–315.

Shanks, A. L. 1985a. Behavioral basis of internal-wave-induced shoreward transport of megalopae of the crab *Pachygrapsus crassipes*. *Mar. Ecol. Prog. Ser.* **24**: 289–295.

Shanks, A. L. 1985b. The effects of larval behavior and distribution on the cross shelf dispersal of coastal crabs. Ph.D. Dissertation, University of California, San Diego. 164 pp.

Simpson, J. H., and J. R. Hunter. 1974. Fronts in the Irish Sea. *Nature* **250**: 404–406.

Simpson, J. H., and R. D. Pingree. 1978. Shallow sea fronts produced by tidal stirring. Pp. 29–42 in *Oceanic Fronts in Coastal Processes,* M. J. Bowman and W. E. Esaias, eds. Springer-Verlag, Berlin.

Strathmann, R. R., E. S. Branscomb, and K. Vedder. 1981. Fatal errors in set as a cost of dispersal and the influence of intertidal flora on set of barnacles. *Oecologia* **48**: 13–18.

Wethey, D. S. 1985. Local and regional variation in settlement and survival in the intertidal barnacle *Semibalanus balanoides:* patterns and consequences. Chapter 13 in *The ecology of Rocky Coasts,* P. G. Moore and R. Seed, eds. Hodder and Stoughton, Sevenoaks, Kent, England.

Winant, C. D. 1974. Internal surges of coastal waters. *J. Geophys. Res.* **79**: 4523–4526.

Winant, C. D., and A. W. Bratkovich. 1981. Temperature and currents on the southern California shelf: a description of the variability. *J. Phys. Oceanogr.* **11**: 71–86.

Winant, C. D., and J. R. Olson. 1976. The vertical structure of coastal currents. *Deep-Sea Res.* **23**: 925–936.

Zeldis, J. R., and J. B. Jillett. 1982. Aggregation of pelagic *Munida gregaria* (Fabricius) (Decapoda, Anomura) by coastal fronts and internal waves. *J. Plankton Res.* **4**: 839–857.